

Observations on the Mating Behavior of Captive Spotted Sand Bass (*Paralabrax maculatofasciatus*)

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Abstract.—The sex allocation pattern of various populations of spotted sand bass are thought to vary from functional gonochorism to strict protogyny. The development of hypotheses explaining how such a plastic (flexible) strategy has been maintained selectively has been hindered by a general lack of information on reproductive behavior in this species. Therefore, the spawning behavior of adult, wild-caught spotted sand bass were observed in captivity under a variety of densities. Three distinct spawning modes were observed: 1) pair spawning, 2) group spawning, and 3) spawning including a sneaker male. Courtship was characterized by the following sequence: 1) a male or males approach the females, 2) one or more males make contact with the ventro-lateral surface of the female and chase the female, 3) the male contacts the ventro-lateral surface of the female and pushes her through a vertical spawning rush. Spawning behavior involved ephemeral color changes, persistent physical contact initiated by the male, short rushes beginning near structure and ending in a vertical rush with a gamete release.

In general, in low density groups, reproductive activity was dominated by a single male that actively excluded smaller males from spawning. The dominant male in these groups exclusively engaged in pair spawning. Individuals in groups of higher density spawned in groups, with no observations of large males monopolizing females.

These observations are consistent with the predictions of the size-advantage hypothesis regarding mating strategies in fishes. We propose that these three spawning modes and the frequency with which they occur allow the flexibility seen in the mating strategies of isolated populations of spotted sand bass.

Introduction

The spotted sand bass, *Paralabrax maculatofasciatus*, is a shallow water seranid that inhabits the bays and lagoons of southern California, Baja California and the Gulf of California. These physically protected areas consist of eelgrass, surfgrass, rock/sand interfaces and serve as warm water refuges for this subtropical species (Allen 1985).

Spotted sand bass spawn in the summer (Allen et al. 1995) and are believed to be multiple spawners (Quast 1968). Oda et al. (1993) suggested that *Paralabrax maculatofasciatus* are capable of spawning on a daily basis. This species forms spawning aggregations at the entrances of bays in southern California, the pelagic

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eggs enter the plankton in coastal waters (Allen et al. 1995), and the juveniles settle out of the water column at 25 to 31 days (Allen, unpubl. data) off southern California.

The spotted sand bass is the only known hermaphrodite among serranids common to southern California (Hastings 1989). However, the sex allocation pattern of various populations of spotted sand bass appear to vary from functional gonochorism to strict protogyny (Hovey and Allen 2000; Hovey et al. 2002). Hastings (1989) found three transitional individuals of this species collected from the northern Gulf of California and confirmed protogyny in that population. Following exhaustive sampling of six sites in California and along both sides of the Baja California Peninsula, Hovey and Allen (2000) also confirmed protogyny in fish sampled from San Diego Bay and Los Pulpos, Baja California (northern Gulf of California). They found five transitional individuals from these two sites. However, fish sampled from both Anaheim and Newport bays in southern California were considered as functionally gonochoric because they lacked transitional individuals and standard demographic patterns, although secondary males were collected at each site (Hovey and Allen 2000). In all populations of spotted sand bass examined, both primary and secondary males were present in all size classes.

Based on these studies, Hovey and Allen (2000) proposed that the size advantage hypothesis (Ghiselin 1969) could explain the reproductive patterns observed for each individual population of spotted sand bass examined. Low density spawning aggregations covering large areas may select for protogynous strategies in populations within San Diego Bay and the northern Gulf of California (Hovey and Allen 2000) because terminal males can dominate spawning activities (Allen et al. 1995). Functionally gonochoric populations, such as those in Anaheim Bay and Newport Bay appear to form dense groups in spatially restricted spawning areas, thereby allowing subordinate males to engage in spawning activities (Hovey and Allen 2000). The hypotheses regarding the impact of low and high density breeding aggregations on reproductive strategy in spotted sand bass have yet to be tested. In fact, prior to the current investigation, basic courtship and spawning behavior had not been described in this species, largely due to the high turbidity of the water in most spawning areas within embayments. Our initial prediction was that the plasticity of mating strategy (gonochorism to protogyny) described in different populations of this sea bass may be maintained by a variety of spawning strategies as seen in several species of wrasses (Warner and Hoffman 1980; Warner 1982 1984, Adreani and Allen, in press).

This paper describes our initial observations on the reproductive behavior of spotted sand bass in captivity. The specific objectives are to: 1) describe courtship and spawning behaviors of adult spotted sand bass and 2) to make preliminary observations on the effects of group size on the mating strategy of this protogynous hermaphrodite.

Materials and Methods

Observation Tank Design

Two types of tanks were used for behavioral observations. The first design used two (T1 and T2) circular 1,100 L indoor, insulated fiberglass tanks set up on a flow through system at the Science, Education, and Adventure Laboratory (SEA

Lab) located on the waterfront of King Harbor, Redondo Beach, California (33° 50.50'N, 118° 23.70'W). Both tanks were illuminated with 120 w plant lights set on timers to regulate the daylight cycle at 14 L:10 D to simulate mid-summer light cycles. Water in each tank was heated with 300-w submersible heaters suspended from two 2" PVC pipes spanning the top of each tank. Each tank was stocked with wild-caught adults from San Diego Bay, California (32° 37.30'N, 117° 14.80'W) collected by hook and line in January 2002.

The second type of observation tank (T3) was a large (11,300 L) mobile aquarium that is equipped with a re-circulating two-stage (chemical and mechanical) filter system. This tank was housed at the Southern California Marine Institute (SCMI) on Terminal Island, in the Port of Los Angeles, California (33° 42.00'N, 118° 12.10'W) and was under natural light conditions. The walls of this tank (T3) are made of 3.8 cm thick transparent acrylic panels permitting a nearly unobstructed view of the fish. Water temperature ranged between 19 and 25 °C during observations. All of the spotted sand bass stocked in T3 were collected from Mission Bay, California (32° 45.54'N, 117°15.38'W) by hook and line in April 2003.

Tank T1 and T2 were stocked at one of two group densities. The T1 group consisted of 26 adults (20 fish/kl), with a minimum of five males (maximum 8 possible), to represent a high-density aggregation. The T2 group included ten adults (9 fish/kl), with three males, to represent a low-density aggregation. The group in T3 was adjusted to simulate several aggregation densities. The first group included eight adults (five females and three males; 0.7 fish/kl) and was observed for 10 nonconsecutive days over a 20 day period. Next, the group was reduced by three fish leaving two males and three females; then observed for eight nonconsecutive days over a 14 day period. Subsequent to the five-fish group (0.4 fish/kl), the group size was increased to 12 individuals (1 fish/kl) by the addition of seven adults (four females and three males). The final group of 12 fish was observed for seven nonconsecutive days over a period of 10 days.

Observation of Spawning

Observations of spawning behavior were made between 1700–2100 hr in tanks T1 and T2 from June to August 2002 and May to June 2003. Observations were made in T3 from August to October 2003. Behavior was observed in the tanks and videotaped with a Canon® digital video camera (Model ZR 45-MC) from a dorso-lateral angle. Various behaviors were catalogued by time of day, frequency, and number of fish involved, as well as the sex of those individuals when possible. Videos were later scored for the type of behavior, duration of interaction, coloration of involved individuals, relative position of individuals in relation to one another, and culmination of event (spawn, aborted rush or end of an agonistic interaction). Discrete, quantifiable acts of behavior were considered to be “bouts”. Behaviors were generally categorized as aggressive, courting, and spawning (pair or group).

Aggressive behavior was defined as one or more fish exhibiting at least one of the following postures: flaring of fins, face off between individuals, high intensity color contrast flash, chasing, jaw snapping, and biting (Erisman and Allen 2005b). Courting behaviors were identified as intense male attention to a female including lateral display, slow following, physical contact by male on the ventro-lateral

surface of female near the abdomen, and rapid movements over the top of the female. Spawning bouts involved a minimum of one male chasing one female in a vertical rush resulting in gamete release (Erisman and Allen 2005b).

Timing and detailed descriptions of courtship and spawning behaviors were recorded from T3 observations because of the increased visibility of these behaviors in comparison to T1 and T2. Pair-spawning events were characterized as only involving two individual fishes, one male and one female. Group spawning events involved three (>2 males and 1 female) or more individuals. Sneak/streak spawning events were therefore included in the group spawning category. Males and females were initially distinguished by sexual dichromatism as described in Allen et al. (1995). Sexual identity was later confirmed by activity and coloration during spawning.

Results

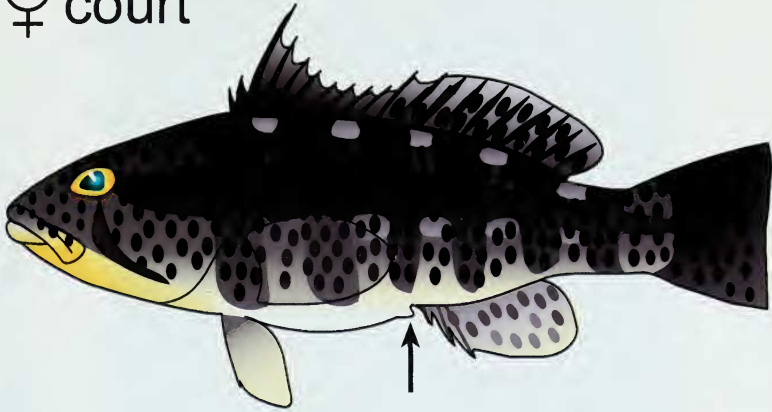
Spawning Modes and Courtship Behavior

During pre-courtship activities, females were dark-bodied, with black bars over a dark green background (Figure 1). During actual courtship and spawning periods, females developed a higher contrast color pattern with the background lightening to light green/off-white. Males exhibited a high-contrast pattern, black bars over a white background during the entire daily spawning period.

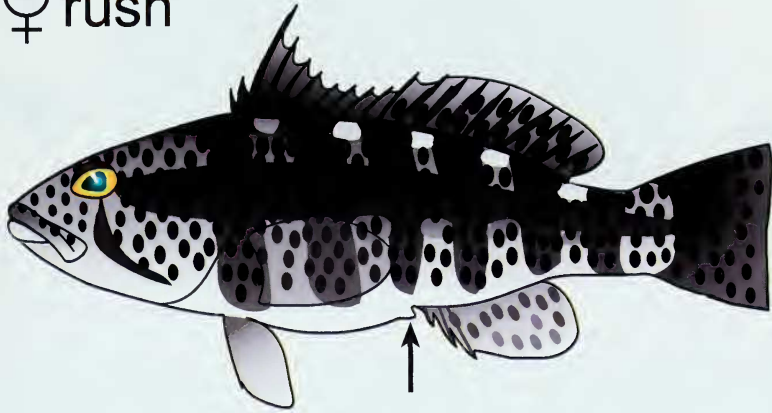
Spawning events were defined as interactions starting with a male initiating courtship by contacting a gravid female on her ventro-lateral surface and culminating in a spawning rush. Three distinct spawning modes were observed: 1) pair spawning, 2) group spawning, and 3) spawning including a sneaker male. Courtship involved one male and one gravid female in 10 of 18 spawning observations. On two occasions, two males were observed courting a female, but courtship followed the same pattern as with one male. No detailed courtship observations were made for the remaining spawning events (6/18) because of insufficient light and/or poor visibility, which prevented video-taping.

In pair spawning events, a courting male initiated contact with a gravid female by approaching from the side (Figure 2A). The female usually responded by swimming away slowly. The male then followed, mirroring the female's movements from behind and underneath (Figure 2B). The male usually moved from one side of the female to the other as he followed. Once the female stopped, she would begin to sink slowly. The male then followed her down, with his snout near her abdomen. Males often made contact with the abdomen of the female during this slow descent. The descent usually stopped about 1 m above the bottom of the tank. The female then raised her head to position her body at a 45° angle to the bottom and changed her color to a high contrast (black bar over a white background) pattern, similar to that of the male. The male then moved beneath the female and began a head-to-tail spiral chase, parallel to the bottom, gradually rising in the water column (Figure 2C). Chase sequences varied in length and speed. Males frequently ceased the chase momentarily, would swim away and then quickly return (Figure 2D). Males made frequent passes over or under the female (Figure 2E). Chasing behavior was common during courtship. During these bouts the male would often make contact with the female and initiate another short chase sequence. In the course of a chase the male often moved up to a

♀ court



♀ rush



♂ court

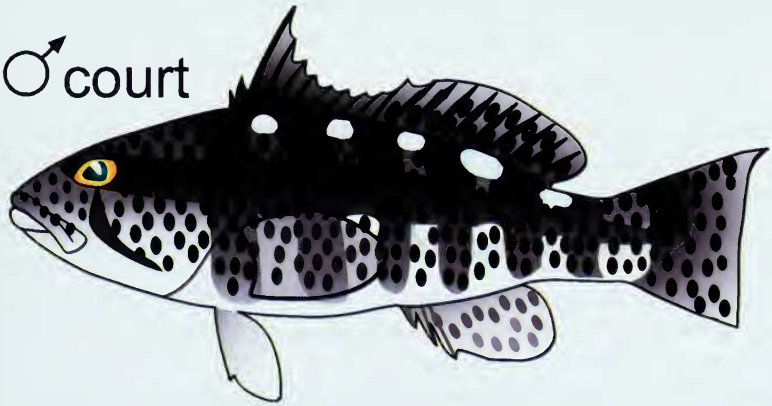


Fig. 1. Courtship-related coloration patterns in *Paralabrax maculatofasciatus*.

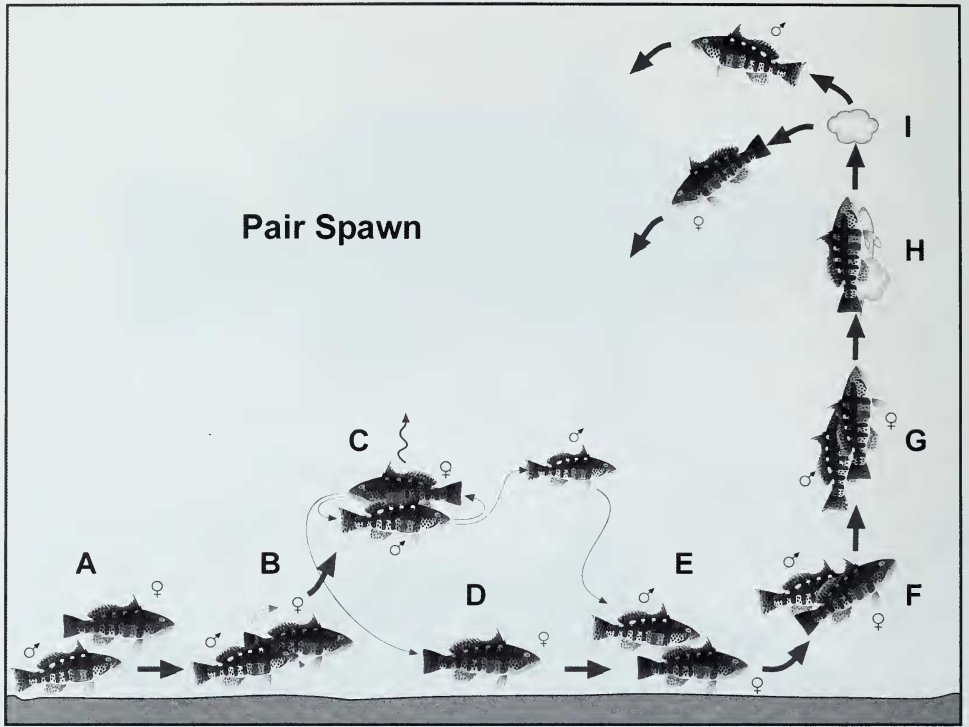


Fig. 2. Diagrammatic representation of *Paralabrax maculatofasciatus* pair spawn from courtship to gamete release. A. Initial contact of gravid female with dark contrast and a yellow chin by a high contrast male. B. Male contacts female abdomen. C. Flat spiral caused by male chasing female. Chase gradually moves vertically in water column. D. Male breaks off chase and leaves area. Female does not move far from position male left her. Male leaves for a short time, then returns quickly. E. The sequence may be repeated several times during a single courtship. F. Spawning pair initiates turn upward to begin spawning rush. Both male and female maintain courtship coloration. G. Spawning rush with both fish take on high contrast pattern. Male takes position with snout pushing at female near insertion point of second dorsal fin. H. Gamete release at near peak of rush. I. Rush peak, gamete cloud present with spawning pair separating. Female regains dark contrast with yellow chin color pattern and returns to structure, while male returns to bottom in search of another gravid female.

position near the origin of her second dorsal fin, and began pushing the female (Figure 3). Once in this position, the male directed the female upwards, initiating a rush to the surface (Figure 2F, G) and subsequent gamete release by both the female and male (Figure 2H). After the gamete release, the fish separated and returned to the bottom (Figure 2I). The females usually returned to shelter, and males began approaching other females, still exhibiting courtship coloration. Males tended to lose their courtship coloration after all females had been approached.

In a typical group spawn, courting males initiated contact with gravid females by approaching from the side (Figure 4). The female responded by swimming away slowly. The group of males converged on the female from all sides initiating a rush to the surface by all fish in the group. After the subsequent gamete release, all fish separated and returned to the bottom.

In a group spawn involving a sneaker male (Figure 5), courtship begins as in



Fig. 3. A male *Paralabrax maculatofasciatus* in the position near the mid-dorsal region of a gravid female just prior to a vertical spawning rush to the surface.

a pair spawn and is later interrupted by a male (sneaker) that joins as the original pair make their vertical turn to begin the spawning rush towards the surface. The sneaker, therefore, joined in the spawning rush and in subsequent gamete release. In one observation of a sneak spawn, the sneaker was observed colliding with and displacing the original courting male in close proximity to the female.

Spawning Times and Coloration

The mean duration of all spawning bouts was 127 seconds (range 45.1–190.1 sec). The mean spawning rush for the captive adults lasted 4 sec, measured from the vertical turn (that terminated courtship) to gamete release.

Spawning was observed from 1745–1945 hr in T3 (Figure 6). Most spawns (83%) occurred after 1900 hr, however, two spawns occurred at 1850 and 1854 hr. Sundown times during the observation period began at 1922 hr and ended at 1853 hr (Figure 5). The mean spawn time for the eight-fish group was 1906 hr (+ 31 min), 12 minutes before sunset (1918 hr). The mean time of spawning for the five-fish group was 1924 hr (+ 10.1 min), 31 min after sunset (1853 hr).

Activity patterns were noticeably different between the sexes. In the late afternoon (1700–1800), females were observed swimming, most frequently near the top of the tank. By 1900, females were less active and their abdomens began to swell. As time progressed, the genital papilla of females with swollen abdomens began to protrude (Figure 7). Males were also less active in the late afternoon, becoming more active as the spawning period approached. During courtship, fe-



Fig. 4. Diagrammatic representation of *Paralabrax maculatofasciatus* group spawn from courtship to gamete release.



Fig. 5. Diagrammatic representation of group spawning in *Paralabrax maculatofasciatus* involving a sneaker. The courtship begins as a pair courtship that is later interrupted by a sneaker that joins as the original pair make their vertical turn to begin the spawning rush towards the surface.

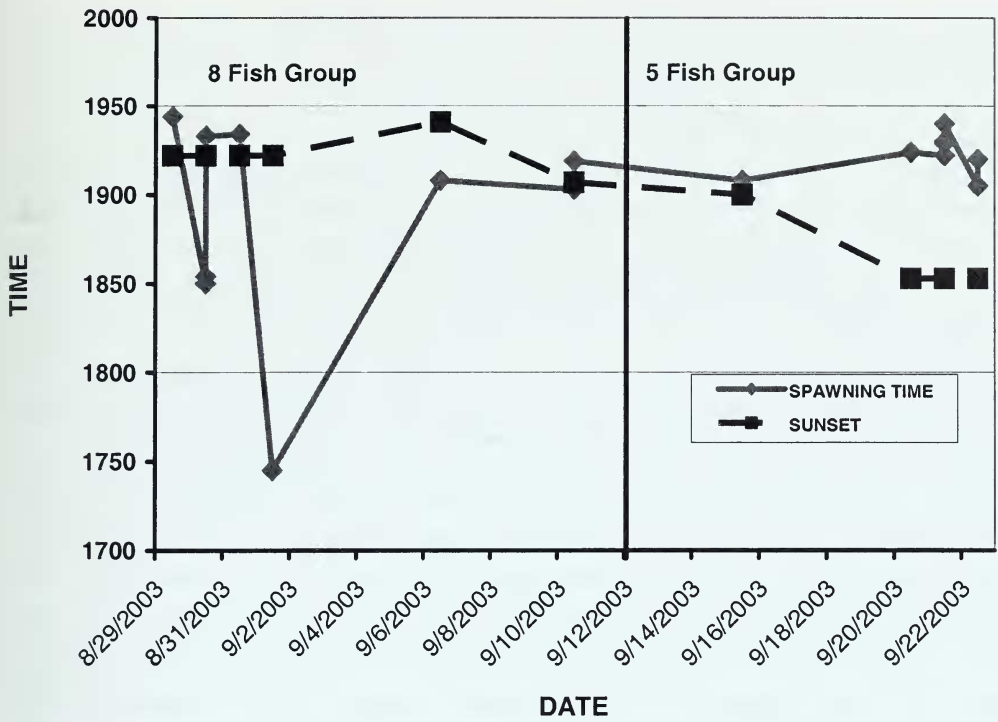


Fig. 6. Spawning and sunset times for the T3 tank observations.

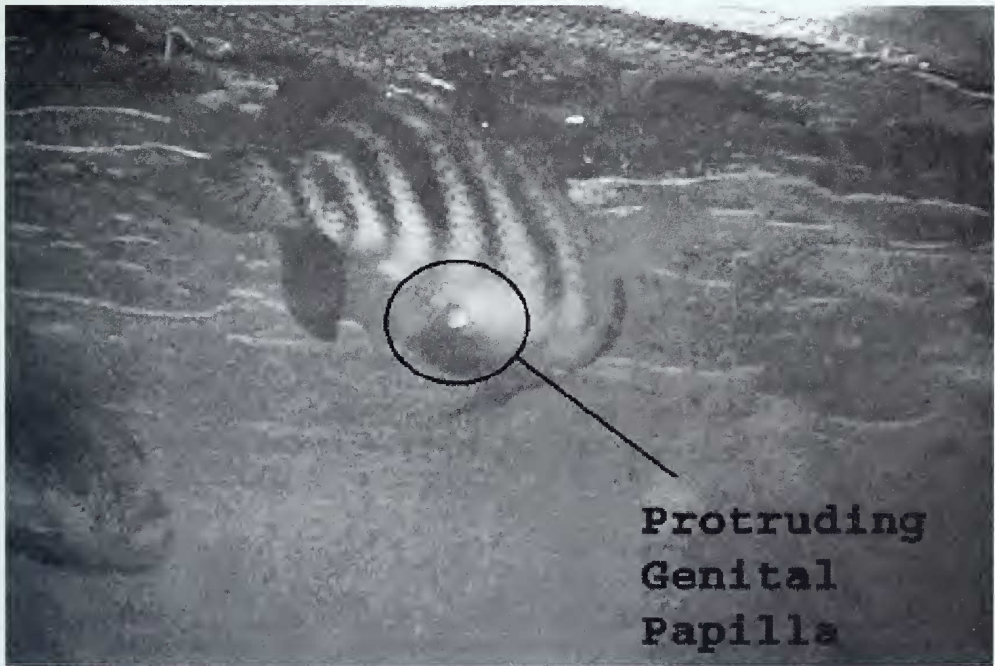


Fig. 7. A large gravid female of *Paralabrax maculatofasciatus* with genital papilla protruding from abdomen prior to being courted by an active male.

males were observed hovering, most often near the bottom, while males began approaching them.

Observations on Spawning Modes and Group Size

Overall, 34 spawning bouts were observed in all three tanks. Eleven of these spawns were observed in T1 (large group = higher density), of which 10 were characterized as group spawns with only one pair-spawning event. Only three agonistic interactions were observed in the T1 group, all lasting less than one minute. Sneak spawning was common (Figure 4), occurring in three of the ten recorded group spawns.

Five spawning events were observed in T2 (small group = lower density). All were pair spawns (Figure 1), with the same male involved in all spawns. This male was observed actively excluding other males, and on three occasions, was observed chasing a subordinate that was engaged in courtship activities with a female. Ten agonistic interactions were observed in T2. A single, dominant male was observed in all of the combative activities, with one other male involved most often (80%) with the dominant male. The interactions between these two males were not limited to spawning periods, and were observed at various times throughout the day. Confrontations between these two males in T2 ranged in duration from short (<1 min.) to very long (>1 hr) with one of the two ending the contest by leaving the area. Most encounters began with a dorsal fin flare and color contrast flash, but could quickly progress into a face off, jaw wrestling, charging and chasing, and finally, in some cases, one fish biting the other.

Eighteen spawning events were observed in T3 with various group densities. Sixteen of the 18 spawning events were pair spawns while two were group spawns involving only two males and one female. Neither of the group spawns included sneakers as both males were observed participating in courtship through the spawning rush. Eleven spawning events were observed when eight fish were in the tank, while seven were witnessed with a group of five fish.

Both pair and group spawning was observed in the eight-fish group in T3. However, pair spawning was more common in this group (9 of 11 spawns). The same male was observed actively courting females when the male could be clearly identified by physical characteristics. Male-male aggression was observed once in the eight-fish group, and three female-female agonistic events were also recorded. Female-female interactions involved a gravid female (swollen abdomen) and a presumably inactive female (not swollen).

When five fish were present in T3, only pair spawning was observed. In this case, all spawns involved the same male, with all females of the group observed to spawn at least once. No agonistic activity was observed in this group.

Discussion

Allen et al. (1995) first documented sexual dichromatism in spotted sand bass as males with high contrast dark bars over a white background with a white chin, whereas females were overall darker with dark bars over a medium toned green-gray background with a yellow chin. These patterns are enhanced during reproductive activities with males accentuating the high contrast, while the females gradually developed a darker pattern with less contrast between bars and general

background. Only during active spawning do the differences disappear as both males and females take on the high contrast patterns normally seen in males only.

Ephemeral color changes have been documented in other serranids (Gilmore and Jones 1992; Erisman and Allen 2005a; Sala et al. 2003). Kodric-Brown (1998) suggests reproductively related ephemeral color changes in fish may assist in coordinating the activities by signaling the breeding state of the participants. In the current study, male and female spotted sand bass were observed to spontaneously alter their color patterns in response to agonistic challenges, reproductive approaches, and spawning rushes. Gilmore and Jones (1992) found similar modifications to occur in scamp (*Mycteroperca phenax*) and gag (*M. microlepis*). Similarly, Erisman and Allen (2005a) observed both seasonal and ephemeral color change in kelp bass related to reproduction. He noted that during courtship, males accentuated their normal breeding coloration whereas females maintained or darkened their coloration. Unlike kelp bass, female spotted sand bass take on a high contrast color pattern, similar to the male pattern, during the final spawning rush.

Spotted sand bass exhibited many similarities in courtship and spawning behavior to that of a partially sympatric congener, the kelp bass (*Paralabrax clathratus*; Erisman and Allen 2005b). Chief among these was the extensive contact between male and female during courtship and spawning in both species. Also, females from both species showed a dramatic decrease in activity when gravid, while the males greatly increased their activity levels during spawning periods. Moreover, definitive color changes occurred in both sexes for both species of *Paralabrax* during courtship and spawning, with an accentuation of the color patterns normally present to indicate reproductive state. The primary difference between the spawning behaviors of the congeners was the occurrence of multiple mating strategies in spotted sand bass.

Shapiro (1987) concluded that inter- and intrasexual behavior was responsible for inducing sex change in the hermaphroditic wrasse, genus *Thalassoma*. Relative size and behavioral interactions of males within a spawning aggregation were believed to be the dominant stimuli for sex change in protogynous fishes (Shapiro 1987). The size-advantage model (Ghiselin 1969), for the evolution of protogynous hermaphroditism, predicts that large males prevent small males from engaging in spawning behaviors, but allow small females to reproduce. Thus, it is advantageous for an individual to be female while small, and change sex when larger (Warner 1984). Warner and Hoffman (1980) detailed the effect of local population size on the effectiveness of male-dominated reproduction in *Thalassoma lucasanum*, and found local population size to be strongly correlated to the effectiveness of male reproductive dominance through territorial defense. In low-density populations, large terminal-phase males were capable of excluding smaller males from females. As population density increased, the ability of terminal-phase males to exclude small males from spawning decreased as tactics such as sneak (streak) spawning increased in frequency (Warner and Hoffman 1980). When the increased energy expenditure for defense of females by a terminal-phase male exceeds the reproductive advantage, the selective advantage of sex change is lost by the individual and, collectively, within the breeding population.

Munoz and Warner (2003) recently modified the size advantage hypothesis for protogynous hermaphroditism. The authors indicated that large females may defer sex change to smaller individuals due to a skew in the size fecundity relationship.

According to Munoz and Warner (2003), the relationship between female body size and fecundity may be logarithmic rather than linear. This predicts that the fecundity of a single, large female may be equivalent to that of all remaining females in a population. In such a case, sex change may not present a reproductive advantage. In addition, sperm competition from sneaker males, which may lessen the dominant male's paternity, further lessens the evolutionary advantage gained by sex change from a large, highly fecund female to a dominant male.

In spotted sand bass, small, low density groups were observed to pair spawn in 91% of observed spawning events. The large, higher density groups engaged in group spawning in 91% of observed events. The size-advantage model for protogynous hermaphrodites predicts that breeding aggregations with relatively low fish density would allow dominant males to monopolize females for spawning activities via pair spawning. Selection would favor a protogynous sex allocation in this case. Conversely, a large, high density breeding aggregation would select for group spawning strategies, as reported for *Paralabrax clathratus* (Erisman and Allen 2005b), where a large dominant male would be incapable of excluding other males from engaging in spawning activities. During brief field observations of a large, dense spawning aggregation in Guerrero Negro, Baja California Sur, Hovey (pers comm³) noted only group spawning to occur. Warner and Hoffman (1980) reported similar results for blueheaded wrasse, *Thalassoma bifasciatum*, where terminal phase males comprised 12% of the population on small reefs but only 1% on larger reefs. Small reefs with low fish density supported pair-spawning aggregations, whereas large reef aggregations with high fish density were observed to group spawn exclusively. Furthermore, Warner (1982) indicated that sex change in the rainbow wrasse, *Thalassoma lucasanum*, was rare, only occurring at low population densities. Low density groups of spotted sand bass may very well show the same pattern (Hovey and Allen 2000).

In summary, the size-advantage model seems to explain the maintenance of multiple mating strategies of (at least captive) spotted sand bass quite well. Behavioral observations of captive fishes in low and high density groups indicated that spawning aggregation density may have a significant influence on the sex allocation of this facultatively protogynous hermaphrodite. In small, low density spawning groups, pair spawning with a single dominant male was the prominent mating strategy observed, thereby making a sex change from female to male selectively advantageous. Large, high density groups primarily displayed group spawning, in which case sex change may offer little or no selective advantage. At higher density levels, large males were not observed to exclude smaller males from engaging in reproductive activities, perhaps suppressing any reproductive advantage that may be gained through post-maturational sex change.

Acknowledgments

The authors would like to thank M. Gardner, M. Miller, B. Tufts, D. Warren, D. Bottinelli, J. Williams, M. Salomon, as well as G. Cetrulo, L. Elkins and the interns of the S. E. A. Laboratory in Redondo Beach, CA for their assistance. We also acknowledge the technical assistance of B. Victor and T. Hovey. This manuscript was greatly improved by the comments of D. Pondella, M. Franklin, R.

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Espinoza, and B. Erisman. This project was generously supported by the following: facilities were provided by the S.E.A. Laboratory in Redondo Beach, CA which was founded by Southern California Edison and the Earth Island Institute, PADI Project A.W.A.R.E. Foundation, Sigma Xi Grant-in-aid, California State University, Northridge Office of Graduate Research and Sponsored Projects through the Graduate Equity Fellowship and Thesis and Performance Grant, and a California State University, Northridge Corporation Student Project Committee grant.

Literature Cited

- Adreani, M. S. and L. G. Allen. In press. Reproductive behavior and mating system of the temperate wrasse, *Halichoeres semicinctus*. J. Fish Biol.
- Allen, L.G. 1985. A habitat analysis of the nearshore marine fishes from Southern California. Bull. So. Calif. Acad. Sci. 84(3): 233–155.
- Allen, L. G., T. E. Hovey, M. S. Love, J. T. W. Smith. 1995. The life history of the spotted sand bass (*Paralabrax maculatofasciatus*) within the Southern California Bight. CalCOFI 36:193–203.
- Erisman, B. E. and L. G. Allen. 2005a. Seasonal and ephemeral color patterns in the kelp bass, *Paralabrax clathratus* (Teleostei: Serranidae). Bull. So. Calif. Acad. Sci. 104(2):45–62.
- Erisman, B. E. and L. G. Allen. 2005b. Reproductive behavior of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, U.S.A. J. Fish Biol. 67:1–29.
- Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. Quart. Rev. Bio. 44:189–208.
- Gilmore, R. G. and R. S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis*, (Goode and Bean) and *M. phenax* Jordan and Swain. Bull. Mar. Sci. 51(1):83–103.
- Hastings, P. A. 1989. Protogynous hermaphroditism in *Paralabrax maculatofasciatus* (Pisces: Serranidae). Copeia 1989:184–88.
- Hovey, C. B., L. G. Allen, and T. E. Hovey. 2002. The reproductive pattern of barred sand bass (*Paralabrax nebulifer*) from southern California. CalCOFI 43:174–181.
- Hovey, T. E. and L. G. Allen. 2000. Reproductive patterns of six populations of the spotted sand bass, *Paralabrax maculatofasciatus*, from southern and Baja California. Copeia 2000:459–468.
- Kodric-Brown, A. 1998. Sexual dichromatism and temporary color changes in the reproduction of fishes. Amer. Zool. 38:70–81.
- Oda, D. L., R. J. Lavenberg, and J. M. Rounds. 1993. Reproductive biology of three California species of *Paralabrax* (Pisces: Serranidae). CalCOFI 34:122–132.
- Sala, E., O. Aburto-Oropeza, G. Paredes, and G. Thompson. 2003. Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bull. Mar. Sci. 72:103–121.
- Shapiro, D. Y. 1987. Differentiation and evolution of sex change in fishes. Bioscience 37:490–497.
- Sokal, R. R. and F. J. Rohlf. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman and Co., New York, NY. 887pp.
- Warner, R. R. 1982. Mating systems, sex change, and sexual demography in the rainbow wrasse, *Thalassoma lucasanum*. Copeia 1982:653–661.
- Warner, R. R. 1984. Mating behavior and hermaphroditism in coral reef fishes. American Scientist 72: 128–136.
- Warner, R. R. and S. G. Hoffman. 1980. Local population size as a determinate of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). Evolution 34:508–518.